

1 **Title: Skewness in bee and flower phenological distributions**

2 Running head: Phenological skews

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28 **Abstract**

29 Phenological distributions are characterized by their central tendency, breadth, and shape, and
30 all three determine the extent to which interacting species overlap in time. Pollination mutualisms rely
31 on temporal co-occurrence of pollinators and their floral resources, and while much work has been
32 done to characterize the shapes of flower phenological distributions, similar studies including
33 pollinators are lacking. Here, we provide the first broad assessment of skewness, a component of
34 distribution shape, for a bee community. We compare skewness in bees to that in flowers, related bee
35 and flower skewness to other properties of their phenology, and quantify the potential consequences of
36 differences in skewness between bees and flowers. Both bee and flower phenologies tend to be right-
37 skewed, with a more exaggerated asymmetry in bees. Early-season species tend to be the most skewed,
38 and this relationship is also stronger in bees than in flowers. Based on a simulation experiment,
39 differences in bee and flower skewness could account for up to 14% of pair-wise overlap differences.
40 Given the potential for interaction loss, we argue that difference in skewness of interacting species is an
41 under-appreciated property of phenological change.

42

43 **Introduction**

44 Timings of seasonal life-history events (phenology), are often characterized by single points in
45 time (e.g., first-appearance date), but in reality these events are typically distributed processes (Carter
46 et al., 2018). Species phenological distributions are characterized by their central tendency, their
47 breadth, and their shape (e.g., mean, standard deviation, and skewness) (Rathcke et al., 1985).
48 Ecological interactions usually require temporal co-occurrence, where the population performance of
49 any species is dependent on phenological overlap with resource availability. In the case of pollination
50 and other mutualistic interactions, interacting species benefit from maximizing temporal overlap with
51 one another, while dealing with the fitness costs of changing their phenology (Visser et al., 2012). The

52 degree of overlap between interacting species is determined by the mean, breadth, and shape of both
53 species' phenological distributions (Fig. 1), with differences in any one of the three properties being
54 enough to reduce overlap. While the shape of phenological distributions has been recognized as an
55 important component of species interactions (Thomson, 1980), studies of phenological match/mismatch
56 in plants and pollinators have focused primarily on how first or mean dates of seasonal activity shift in
57 response to varying cues (Inouye et al., 2019) and how the temporal breadth of their activity stretches
58 or contracts. The importance of skewness differences in determining mismatch in pollination
59 interactions remains unclear. This is in part because there has not been a systemic analysis of skewness
60 in phenological distributions across many species of pollinators and flowering plants together.

61 Flower phenological distributions are often right-skewed, with a long, trailing tail after the peak
62 of flowering in prairie (Rabinowitz et al., 1981) and montane (Thomson, 1980) ecosystems. Within
63 populations, the degree of skewness can vary among years (Blionis et al., 2001; Forrest et al., 2010).
64 Phenological distribution shape may also be affected by local resource competition that reduces plant
65 size, which is in turn correlated with floral phenology skewness (Schmitt, 1983). It has also been
66 suggested that the right-skewness of flowering phenologies may be a product of selective pressure for
67 early flowering (Forrest et al., 2010) and that recent climate change has affected the shapes of flower
68 phenological distributions (CaraDonna et al., 2014). While the typical patterns of flower phenological
69 skewness are well understood, we do not know if these patterns are also similar for pollinators. There is
70 reason to suspect that phenological sensitivity differs between plants and pollinators and that the
71 seasonal onset and end of activity in pollinators (such as bees) shift at different rates (Stemkovski et al.,
72 2020). Thus, a community-wide assessment to compare bee and flower phenological skewness is
73 warranted.

74 In this study, we quantified phenological skewness for multiple bee and flower species within a
75 montane community. We determined the relative prevalence of right-skewed, left-skewed, and

76 symmetrical distributions, and examined the differences between bees and flowers in how skewness
77 relates to other properties of their phenological distributions. *A priori*, we predicted that bee
78 phenologies would be similarly skewed to those of flowers, but that bees active in the early season
79 would have phenologies more strongly right-skewed than that in the late season due to a hard limit on
80 activity before snowmelt in the study system. Lastly, we performed a simulation study to gain
81 perspective on the potential consequences that variation in skewness in this community may have on
82 phenological overlap between bees and flowers.

83

84 **Methods**

85 *Data sources*

86 We used flower phenology data from a long-term monitoring program spanning from 1974 to
87 2019 at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA, a mountainous
88 location with a short summer growing season set ~2890 m above sea level (CaraDonna et al., 2014;
89 Inouye, 2008). The total number of flowers was counted approx. three times per week for the extent of
90 the growing season for all flowering species in 4 m² fixed plots. This dataset includes mainly long-lived
91 perennial forb species. Further details on this program are reported by CaraDonna et al. (2014) and
92 Inouye (2008), and all data are available through Open Science Framework (<https://osf.io/hy59v/>). For
93 our analysis, we included 35 flower plots aggregated into 8 sites by proximity to agree with the spatial
94 scale of the bee phenology sites. We obtained bee phenology data from a companion study to the
95 flower phenology project which tracked bee abundance from 2009 to 2020 at the RMBL (Ogilvie et al.,
96 2017; Stemkovski et al., 2020). Bee abundance was measured using pan traps approx. every two weeks
97 across the growing season at 18 sites spaced across an elevation gradient (Gezon et al., 2015). Because
98 pan traps are biased toward collecting smaller-bodied bees, hand netting was used for bumble bees
99 (*Bombus* spp.). Additional details on bee data collection and all data are available through Open

100 Science Framework (<https://osf.io/kmxyn/>). All data processing steps and analyses for this study can be
101 viewed and reproduced using code available online (https://github.com/stemkov/pheno_skew).

102

103 *Data processing*

104 We formatted and standardized flower and bee data to make them directly comparable. For all
105 data, we excluded records with uncertain identifications and those that were identified only to genus.
106 We excluded all grass and sedge species, but included shrubs. The bee abundance data were derived
107 from multiple pan traps or netters, so we aggregated flower and bee counts across plots/traps/netters per
108 site. For the bee data, we included only female bees because female specimen identifications were
109 more fully resolved and because combining females and males could lead to inaccurate estimates of
110 skewness when the two sexes have different phenological patterns (as in social species). We
111 distinguished queen and worker castes of bumble bees (*Bombus spp.*) to avoid biasing skewness
112 estimation by confounding an early-season queen peak in abundance and a later peak in worker
113 abundance. Because bumble bees were sampled explicitly by netting and due to difficulties of
114 combining sampling effort between netting and pan traps, we excluded pan-trapped *Bombus* and net-
115 trapped non-*Bombus* bees. To ensure that we only included sampling periods that consistently captured
116 representative samples of abundance, we excluded sampling days when traps were deployed for less
117 than three hours and excluded netting days with less than one hour of effort (excluding 17 of 778 trap
118 sampling days and 21 of 809 net sampling days). Lastly, to ensure adequate sample size and robust
119 skewness estimation, we only considered time-series with at least 10 individual bee records and at least
120 100 flower records. Thus, we excluded 1,932 of 18,710 bee records (10.3%) and 126,659 of 3,943,796
121 flower records (3.2%).

122

123 *Skewness calculation and predictors*

124 We calculated skewness as the Fisher-Pearson standardized third-moment coefficient of
125 skewness (g_1), as implemented in the *moments* R-package (Komsta et al., 2015), for each
126 site/year/species phenological abundance distribution (i.e., frequencies of bee and flower abundance by
127 date). We tested whether skewness was different from zero (corresponding to a symmetrical
128 distribution) using D'Agostino's K^2 test (D'Agostino, 1970).

129 In order to examine whether and how skewness in bees and flowers was related to other
130 properties of their phenological abundance distributions, we calculated the means and standard
131 deviations of each distribution. To test whether the phenological position of species (how early or late
132 they are active in a season) predicted their skewness, we modeled skewness as a linear function of
133 phenological mean interacting with guild (flowers vs. bees). We note that, statistically, means are
134 shifted by skewness, so the two are necessarily linked to a certain extent. To test whether species with
135 longer active seasons tended to be more skewed, we modeled absolute skewness as a linear function of
136 distributions' standard deviation interacting with guilds.

137

138 *Overlap calculation*

139 To demonstrate the potential phenological match/mismatch consequences of skewness
140 differences between bees and flowers, we calculated the maximum possible overlap of distributions
141 with different skews. To do this, we repeatedly generated probability densities of two skew-normal
142 distributions (Azzalini, 2020) with two different skewness parameters and 2000 possible mean and
143 standard deviation parameter combinations each. For each mean and standard deviation value, we then
144 calculated the overlap coefficient (Inman et al., 1989) by integrating to find the area encompassed by
145 both probability density curves (as illustrated in Fig. 1), and recorded the largest of the resulting
146 overlap coefficients. We repeated this procedure for every pairwise combination of 50 skewness values
147 sequenced evenly between -5 and 5, resulting in 2500 (i.e., 50^2) total comparisons. In other words, we

148 calculated the largest possible overlap of paired distributions by keeping skewness constant and
149 allowing mean and standard deviation to vary freely. To provide perspective, we calculated the bounds
150 of the middle 95% of skewness values of bees and flowers from the Rocky Mountain dataset and
151 overlaid these onto the simulated overlap estimates.

152

153 **Results**

154 We estimated skewness for 3,024 flower time-series and 480 bee time-series. The time-series
155 represented 106 plant species across 82 genera, and 49 bee species across 14 genera. In time-series with
156 sufficient data to calculate skewness, the average flowering period (across all years, sites, and species)
157 was centered on July 10, and bee foraging on July 2. The typical flowering breadth, measured as one
158 standard deviation on either side of center, was 14 days in flowers and 39 days in bees. Flower time-
159 series were significantly right-skewed ($g_1 = 0.31$, $t_{3502} = 20.43$, $p < 0.01$), and bee time-series were also
160 right skewed ($g_1 = 0.89$), significantly more so than flowers ($t_{3502} = 13.84$, $p < 0.01$). Viewed
161 individually, 47.6% of flower time-series were significantly right-skewed, only 14% were significantly
162 left-skewed, and 38.5% were not significantly different from symmetrical. Of bee time-series, 48.5%
163 were significantly right-skewed, 9.4% were left-skewed, and 42.1% were symmetrical (Fig. 2).
164 Skewness was somewhat affected by data truncation, though both bees and flower curves were still
165 right-skewed regardless of truncation type (Appendix S1: Section 1).

166 Skewness in plants was significantly predicted by how early or late in the season a species
167 flowered, with early season species being more strongly right-skewed ($t_{3500} = -6.77$, $p < 0.01$). This
168 relationship was more pronounced in bees ($t_{3500} = -22.8$, $p < 0.01$), with early season bees being right-
169 skewed, and later-season bees being left-skewed (Fig. 3, left panel). Plants with longer flowering
170 periods tended to be more skewed ($t_{3500} = 9.32$, $p < 0.01$), while bees with longer active periods tended
171 to be less skewed ($t_{3500} = -11.75$, $p < 0.01$) (Fig. 3, right panel). We do not directly compare bee and

172 flower distribution breadth because the frequency of bee data collection inherently discounted species
173 with short active periods. Hypothetical overlap losses between interacting species ranged from 0% at
174 perfectly matched skewness values to 25% for distributions where one has $g_1 = 5$ and the other $g_1 = -5$
175 (Fig. 4). The maximum overlap loss for the central 95% of bee and flower skewness values found in
176 our datasets was 14% overlap loss. Comprehensive species lists and summary statistics are provided in
177 Appendix S1: Section 3.

178

179 **Discussion**

180 We found that both bee and flower phenological distributions tend to be right-skewed (Fig. 2),
181 suggesting that similar processes are acting on bees and plants to determine the shape of their
182 phenological distributions. Multiple explanations have been offered for skewness in flowering time,
183 including selection for skewed flowering driven by pollinators and resources (Forrest et al., 2010;
184 Thomson, 1980), by-products of intraspecific competition (Schmitt, 1983), and simple geometrical
185 necessity because daily survival probabilities are cumulative and inherently skewed (Blionis et al.,
186 2001). We can identify multiple, distinct scenarios that may lead to skewed phenological distributions
187 by focusing on onset rates (e.g., flower opening, bee emergence) and cessation rates (e.g., floral
188 senescence, bee mortality). First, differences in the intra-annual dispersion of onset and cessation rates
189 may produce phenological skewness. Second, variable phenology among individuals with unequal
190 representation (e.g., different numbers of flowers per individual plant) may produce skewed aggregate
191 distributions even when the component onset and end rates are equally dispersed. Third, onset and/or
192 cessation distributions themselves may be skewed. Further, combinations of these processes may
193 influence the shapes of phenological distributions in complex ways. In the context of our findings, the
194 prevalence of right-skewness in bee phenological distributions suggests that, on average, bees emerge
195 with more synchrony than with which they cease foraging. Drawing conclusions about the processes

196 behind the observed skewness in flower phenology is more difficult due to flower counts being
197 aggregated across individual plants in our data.

198 While demographic data (i.e., tracking individual plants and insects) beyond what we present
199 here are needed to determine the mechanistic causes of the differences in onset/end variance that
200 produce skewed phenology, some information can be gleaned by comparing skewness with other
201 phenological properties. We found that bees that were active closer to the beginning of the growing
202 season tended to be more right-skewed (Fig. 3). For example, the early season sweat bee *Lasioglossum*
203 *sedii*, with an average capture date of June 16 across all sites and years, was strongly right-skewed ($g_1 =$
204 1.94), while the later-season masked bee *Hylaeus annulatus*, with a capture date of August 5 on
205 average, tended to be left-skewed ($g_1 = -0.27$). A similar but weaker pattern was seen in flowers, though
206 flowers did not tend to flip to left-skewness at the end of the season. In the snowy sub-alpine
207 environment of the present study, the onset of activity is strongly limited for flowers (Inouye, 2008)
208 and bees (Stemkovski et al., 2020) by the timing of snowmelt. Because species closer in time to this
209 unambiguous onset cue tended to be more strongly right-skewed, we can reasonably infer that this cue,
210 or at least the phenological response of species to this cue, is less variable than the processes that lead
211 to flower senescence and the end of bee foraging (e.g., frost events, precipitation, inherent
212 lifespan/persistence, etc.). By extension, these findings suggest that later-season onset cues, or species'
213 phenological responses to them, are more variable than the early snowmelt cue.

214 Our finding of right-skewness in flowering phenology was broadly similar to previously
215 published results, though we found that average flowering skewness in the present study ($g_1 = 0.31$)
216 was less positively skewed than in a previous study in the same area ($g_1 = 0.46$; Thomson, 1980) and a
217 prairie community ($g_1 = 0.41$, Rabinowitz et al., 1981). While this comparison is useful, we caution
218 against over-interpretation due to differences between the studies such as duration of monitoring and
219 size of sampling plots. Turning to insects, we lack other studies focused specifically on phenological

220 skewness in other insect groups, but individual abundance time-series indicate that right-skewness may
221 also be found in univoltine butterflies (Dennis et al., 2017; Scott et al., 1987; Zonneveld, 1991), flies
222 (Haab et al., 2019; Judd et al., 1991), and hemipterans (Gamarra et al., 2020; Ma et al., 2008).
223 Comparisons with multi-voltine species in areas with longer growing seasons are difficult, and further
224 research is needed to compare uni- and multi-modal phenological distributions, especially as climate
225 change creates opportunities for additional generations in some insects (Dyck et al., 2015; Hodgson et
226 al., 2011). Given the apparent prevalence of skewness in phenological distributions, we encourage
227 researchers to use modeling methods that are designed to capture asymmetry (Belitz et al., 2020). We
228 advise caution when closely comparing skewness values between bees and flowers because there is
229 inherently more uncertainty in the bee dataset due to the methodological challenges of tracking wild
230 insects.

231 The consequences of variable skewness in flower and pollinator distributions for phenological
232 match/mismatch in natural populations are not well understood and require further study. When
233 considering simulated pair-wise interactions, the skewness of phenological distributions alone has the
234 potential to cause up to 14% loss in overlap in the species that we studied (Fig. 4). We note that this
235 analysis encompassed only phenological differences, and in reality there are other barriers to
236 pollination such as specialization or morphological limitations to pollination. It is also important to
237 consider that loss of overlap does not necessarily translate to fitness losses, as pollen limitation is not
238 ubiquitous (Knight et al., 2005) and many bees and flowering plants are generalists (Waser et al.,
239 1996). Beyond pollination interactions, differences in skewness have the potential to affect other
240 mutualistic interactions, predator-prey and host-parasite interactions, and to alter patterns of inter- and
241 intra-specific competition within guilds. As both flowers and bees tend to be right-skewed, individuals
242 may compete most strongly with their conspecifics in the early part of their activity. Future studies

243 should examine how phenological skewness translates into fitness consequences through changes in
244 inter- and intra-specific interactions throughout species' active periods.

245

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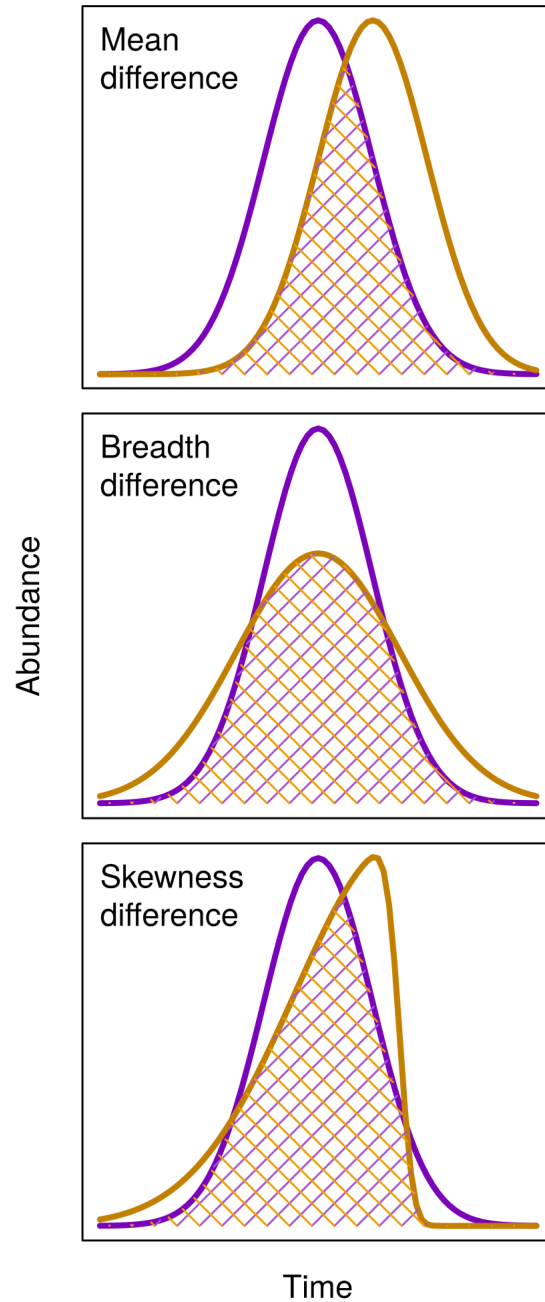
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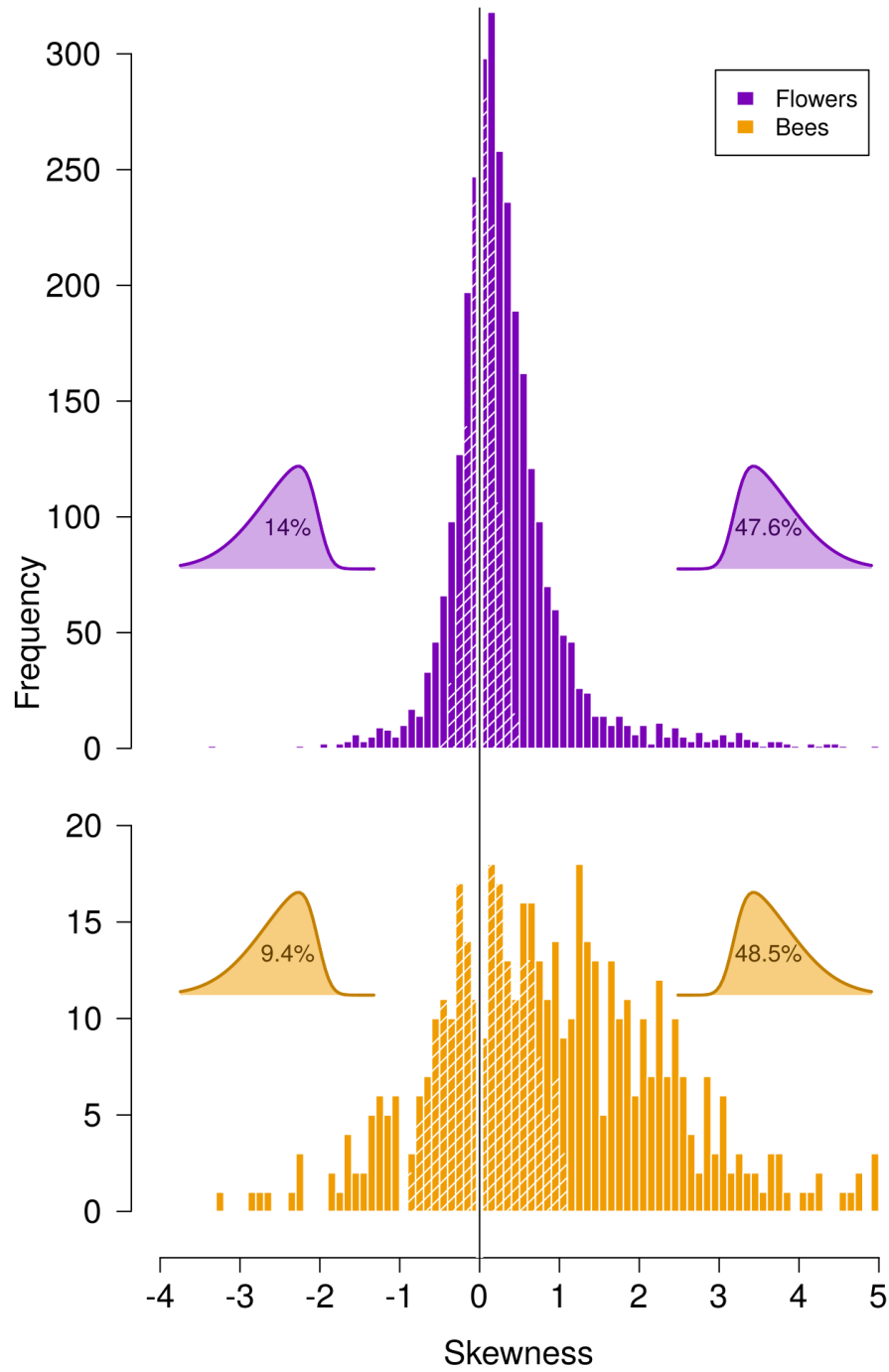
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344 **Figure 1.** Conceptual diagram of the causes of phenological mismatch. Differences in the phenological
345 mean timing (top panel), breadth (center panel), and skewness (bottom panel) of species determine the
346 extent to which interacting species overlap in time. The purple and yellow curves represent
347 phenological distributions of two species, and the hatched areas are times of phenological overlap.

348

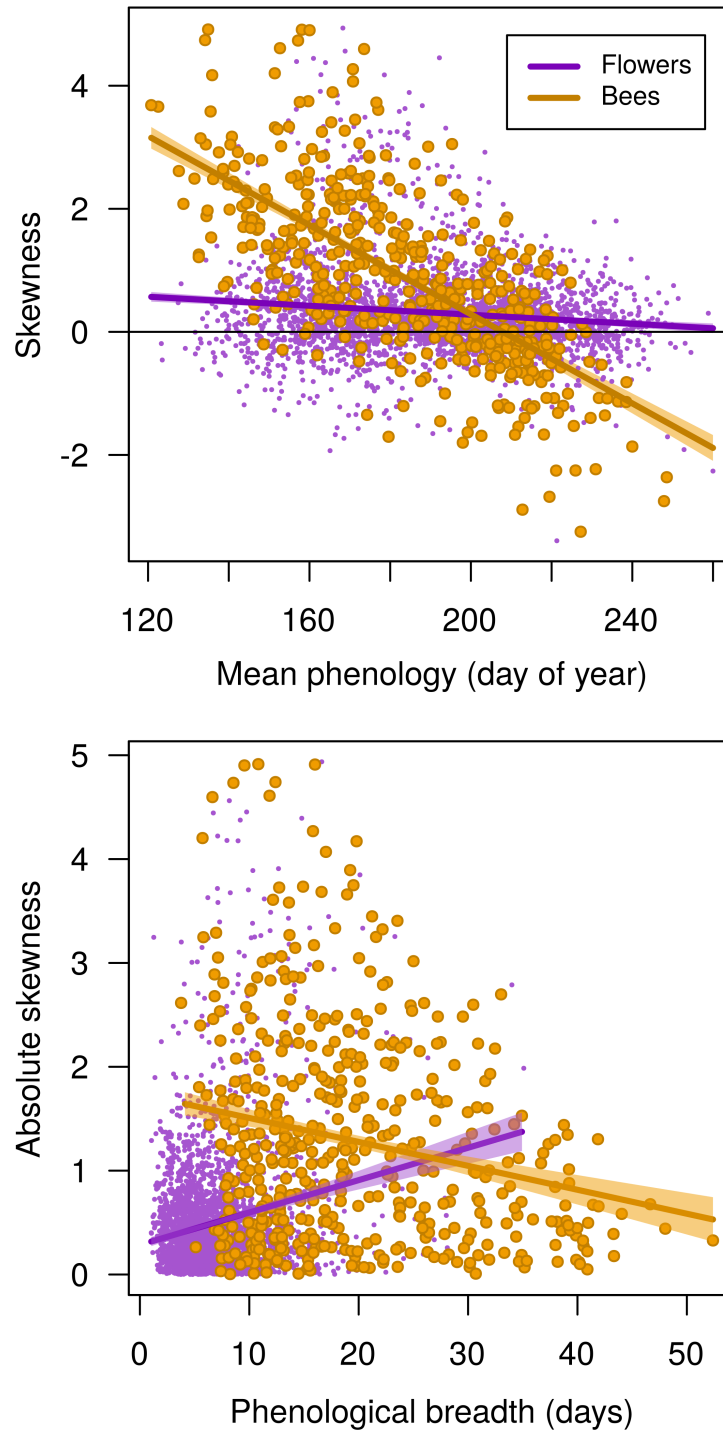


349 **Figure 2.** Flower (top panel) and bee (bottom panel) phenological skewness. Both flower and bee
350 species tend to have right-skewed phenological distributions, though there is substantial variation in
351 shape, and most distributions in both groups are not significantly different from symmetrical. Skewed
352 distribution icons give the percent of individual time-series that are significantly left- and right-skewed.
353



354 **Figure 3.** Skewness is predicted by mean and breadth. Early-season bees and flowers tended to be
355 more heavily right-skewed (top panel), though the effect was more pronounced in bees than in flowers.
356 Flowers with broader phenological distributions tended to be more skewed, while bees with broader
357 phenology tend to be less skewed in either direction (bottom panel).

358



359 **Figure 4.** Skewness constrains the degree to which phenological distributions can overlap. The
360 maximum possible overlap of pair-wise interacting species with different hypothetical skewness values
361 is shown as colors, with red depicting the lowest overlap, and white depicting perfect overlap. Bounds
362 for 95% of the actual observed skewness values are shown with purple lines for flowers, and gold lines
363 for bees. The resulting box in the middle of the figure therefore depicts the potential loss of
364 phenological overlap in pair-wise interactions between bees and flowers due to differences in skewness
365 alone, isolated from the effects of mean and breadth changes.

